

December 13, 1898.

Prof. G. B. HOWES, F.R.S., V.P., in the Chair.

The Secretary read the following report on the additions to the Society's Menagerie during the month of November 1898 :—

The total number of registered additions to the Society's Menagerie during the month of November was 66, of which 23 were by presentation, 14 by birth, 10 by purchase, and 19 were received on deposit. The total number of departures during the same period, by death and removals, was 106.

The following extract was read from a letter from Mr. Stanley S. Flower, F.Z.S. (dated Gizeh, Egypt, Oct. 27, 1898), in reference to the locality of the Siamang (*Hylobates syndactylus*) which he had presented to the Society on the 17th of October.

"This Siamang was caught in Negri Sembilan, a Malay state (or rather a federation of little kingdoms) which lies north of the settlement of Malacca, and south of the important Malay state of Selangor; it is bounded on the east by Pahang, and cut off from the sea to the west by a little state called Sungei Ujong. In the Malay Peninsula the Siamang seems to be very local; in Perak it is found south of the Perak River, but not apparently anywhere north of it. There are stuffed Siamangs in the Taipang Museum, but all were brought from Kinta in the south. The Siamang certainly does not occur in either Penang or Singapore; but specimens are sometimes brought to Singapore from Sumatra, which is the only other place that I have heard of where they are found wild."

Dr. Henry Woodward, F.R.S., exhibited and made remarks upon a remarkably abnormal pair of antlers of the Red Deer.

The following papers were read :—

1. On certain Characters of reproduced Appendages in Arthropoda, particularly in the *Blattidæ*. By H. H. BRINDLEY, M.A., St. John's College, Cambridge¹.

[Received October 19, 1898.]

(Plate LVIII.)

In a previous communication (15) I have given an account of some observations and experiments in connection with the reproduction of the legs in the *Blattidæ*, by which it seems established that, in an individual which has not completed its post-embryonic development, amputation or injury of a leg at

¹ Communicated by W. BATESON, F.Z.S.

any point from the femoro-trochanteric suture downwards is followed by the reproduction of the lost parts, with the distinguishing feature that the tarsus consists invariably of only four joints, the normal congenital tarsus possessing five. The present paper is concerned with the structure of the four-jointed tarsus of reproduction, and with cases of reproduction of appendages in other Arthropods with which it possesses certain features in common. In this connection it is desirable to make some reference to the condition of our knowledge of the reproduction of appendages among Arthropods generally. The literature of the subject does not seem to be extensive. Thirty years ago Milne-Edwards (59) summarized the work then published, and since that time the subject has received only sparse attention, especially from the standpoint of experiment. But certain facts have received satisfactory demonstration. [Among Arthropod animals reproduction is always confined to the appendages. Reproduction of portions of the trunk, as is common in the segmented worms, appears never to occur.]

THE PERIOD OF THE LIFE-HISTORY DURING WHICH REPRODUCTION OF THE APPENDAGES CAN OCCUR

appears to be coincident with that of the ecdyses. Hence in Crustacea and Myriapoda the power of reproducing the appendages continues after the attainment of sexual maturity, while in Arachnida and Insecta it ceases with the completion of the post-embryonic development. But in view of the little that is known of the life-histories and ecdyses of Thysanura, Collembola, and some Orthoptera, the above statement must be made with some reserve as regards the Insecta. It is, however, certain that in the case of most of the groups no reproduction of appendages can occur after sexual maturity has been attained, either through a series of ecdyses or on emergence from a pupal state. As regards *Peripatus*, Mr. Adam Sedgwick kindly informs me that he knows of no instances of reproduction of any of the appendages, or of any cases in which an appendage presented features suggesting that it had been reproduced. If regeneration does occur in this isolated genus, a knowledge of its features would be of special interest.

THE PARTS OF AN APPENDAGE FROM WHICH REPRODUCTION CAN COMMENCE.

If an appendage is *wholly* removed from the body it seems that reproduction never occurs. Thus in a crustacean the coxopodite of an appendage, in an insect the scape of an antenna or the coxa of a leg, must be left intact if there is to be reproduction of the extremity. An appendage is therefore never reproduced as a whole by the trunk, but the event is really the formation of a new extremity by a larger or smaller basal portion. Accidental injury to an appendage may theoretically involve any degree of

loss, but the distribution of possible starting-points of reproduction is particulate, being in all cases controlled by the effects of injury or amputation on the portion left attached to the body. Thus in cases where autotomy at a particular region is the invariable result of injury or amputation in any more distal region, it is obvious that the starting-point of reproduction is localized to the spot where the autotomous break occurs. On the other hand, there are cases in which reproduction seems to commence from the actual extremity left on amputation, so that there is no clear localization of the reproductive power.

There are also certain conditions intermediate between the above extremes. As there is such an obvious relationship between autotomy and the reproduction of lost parts, it is unfortunate that our knowledge of the factors controlling the former event should be so imperfect. The term autotomy has received what seems an undesirably wide application by Giard (35) in an attempt to classify many different phenomena under this title, but in what follows its use is confined to the sudden separation of an appendage or part of an appendage in obvious response to an external stimulus. That the event is truly a reflex action, and therefore dependent on the integrity of the nervous system, has been shown experimentally for the legs of several genera of Decapod Crustaceans by the exhaustive experiments by Frédéricq (26, 27, 28), and for the legs of *Locusta* by Frédéricq (29, 30) and Contejean (19).

In the case of other Arthropods the phenomenon is probably of essentially similar nature. But when a series of experiments is conducted on a particular appendage of a single species, the general experience has been that the latent period which elapses between the application of the stimulus and the rupture varies within wide limits; and not only is this the case, but it is also usually found that though a certain degree of injury or amputation in the distal portion of an appendage liable to autotomous loss will almost invariably bring about quite readily the loss of the remaining portion, it does not always do so, though the stump may break away at the usual seat of autotomy after the lapse of a day or two. So much has been said to indicate that it is after all not at present possible to draw any satisfactory distinction between autotomy in the strict sense and the dropping away of the stump of an appendage some time after the loss of the distal portion, which latter event is of common occurrence in some forms which do not ever exhibit autotomy as defined above. And a satisfactory conception of autotomy is also rendered difficult by the fact that in cases where its occurrence is characteristic, even what are apparently the most favourable conditions will sometimes fail to induce it. The whole subject offers much difficulty, but enough has been said to show that it cannot be left out of account in connection with the reproduction of appendages.

CRUSTACEA.—Among Arthropods autotomy and subsequent reproduction have received the greatest degree of attention in the case of the *thoracic limbs* of Decapod Crustacea. On the authority of Hallez (45) it appears that the earliest observations in detail are

those of Réaumur himself on the *legs* of *Palinurus* and those quoted by him as having been performed on Crabs at Guadaloupe by Le Père de Tertres. Réaumur (69, 70) noted that the autotomous rupture always occurred at the groove marking the fusion of the ischiopodite to the basipodite. [The meaning of this peculiar fusion between two leg-joints in Crustaceans and many Tracheates has recently been discussed by Bordage (9).] Réaumur's observation has been often confirmed for all Decapods which exhibit autotomy. Sixty years later the subject was studied by Bodier (4), while during the present century further observations on Decapods have been made by MacCulloch (56), Heineken (46, 47), Couch (21), Goodsir (38), Spence Bate (1), Chantry (18), Putnam (68), Howes (51), and Brook (17). Milne-Edwards (59) and Huxley (52) have discussed the phenomena described¹. During the last few years more extended experiments on autotomy in particular have been made by Frédéricq (*loc. cit.*), De Varigny (74), and Parize (63). It seems certain that the act is reflex in nature; but on other points there is much disagreement among authors, especially whether it is necessary for the limb to come into sharp contact with the carapace. In *Astacus* a few experiments by myself tend to show that the comparatively feeble autotomy of this genus is exhibited only when the carapace is employed as a *point d'appui*. But in this, as in other Decapods, the results of experiments on autotomy are much influenced by the age and general condition of the animal and by the mode of stimulation employed. There is, however, no doubt that most Decapods have a certain region of the limb specialized for autotomous loss, and with this condition has arisen the localization of regeneration. Pouchet (66) and others have pointed out that the loss of a limb at the suture entails comparatively very slight bleeding. It has often been noticed that injury to more distal portions not followed by autotomy results in the eventual loss of all parts up to the suture, though in *Astacus* I have seen distal joints retained two months after mutilation. Goodsir (38) has given a description of a special structure in the basipodite of *Carcinus*, which he regarded as an organ for producing new limbs. The account, however, seems to require confirmation. But whether the regenerative power is localized as above in those Decapods which do not appear to perform autotomy, such as *Crangon*, *Palæmon*, and the young of *Pagurus* (74), is at present uncertain. Moreover, it is doubtful whether the flagellum (endopodite) of the *antenna* of Decapods exhibits true autotomy, and whether regeneration is confined to the protopodite, or may commence more distally. In *Homarus* Brook (17) has mentioned a "throwing off" of the flagellum, and its complete regeneration has been observed by several authors.

ARACHNIDA. *Araneidae*.—Experiments on autotomy and regeneration were made on Spiders by Heineken (46, 47), who found that reflex casting of the *walking-legs* occurred invariably at the suture marking the fusion of femur and coxa. He considered that a

¹ See also Morgan, *Zoöl. Bulletin*, May 1898.

point d'appui was always necessary for rupture, but in other respects his results were very varied. Autotomy did not always occur in a series of individuals of one species, the latent period between stimulus and loss varied greatly, and the results were greatly affected by age and the mode of stimulus, as well as by the particular genera and families employed. Parize (63) has also observed diversities of this kind. In *Tarantula* it has been shown by McCook (57) that the struggles at ecdysis may result in loss of limbs either at distal regions or at the suture. Blackwall (3), who made numerous experiments on regeneration, has not described either autotomous or eventual loss of the stumps of limbs left after partial amputation. More recently Wagner (75, 76) has made experiments on *Tarantula* with the result that section of a leg about its middle is nearly always followed by the animal tearing out the stump up to the suture, an act which seems to be performed in order to prevent loss of blood, which is, as in other Arthropods, great at the point of section, but very slight at the suture. His experiments also lead him to the important and suggestive conclusion that in cases where the stump is not torn off all its tissues degenerate up to the suture, and that therefore regeneration takes place only from the coxa. But as there is no doubt that there is among Spiders much variation of autotomy, it is possible that in some forms regeneration may commence from points distal to the suture.

Scorpionidae.—Mr. R. I. Pocock informs me that it is practically certain that autotomy does not occur in this group, nor has any account of the regeneration of lost appendages been published. He has, however, examined certain specimens in the British Museum, whose history is unknown, but which are almost certainly instances of partial regeneration of the *walking-legs*. Two of these cases have recently been kindly shown to me by Mr. Pocock, and certainly suggest that in Scorpions regeneration commences from the actual seat of injury and is not confined to one particular region of a limb.

MYRIAPODA.—On the regeneration of appendages in Myriapoda but few observations are recorded, and none are of recent date. Autotomy does not seem to occur in this group. Newport (61) found that in *Julus* the stump of an *antennal* joint was retained, and he concluded that reproduction commenced from the point of amputation, for after ecdysis the regenerated extremity could be clearly distinguished by its lighter colour. In both *Julus* and *Lithobius* he observed *legs* regenerated from the coxa after loss brought about by unknown causes.

INSECTA.—Among Insecta the reproduction of lost appendages is known to occur in certain genera of Collembola, Orthoptera, Hemiptera, and Lepidoptera.

Collembola.—Very little is known concerning the life-histories of the Collembola, but it appears that the ecdyses and the power of reproducing the appendages are continued after full growth and sexual maturity have been attained. In these respects, therefore, the group stands in contrast with other Insecta. In

Collembola nothing is known concerning autotomy, and only the reproduction of the *antennæ* has been studied. Bourlet (14) and in greater detail Lubbock (55) have made observations in this case, and concluded that regeneration seemed to commence from the actual point of amputation.

Orthoptera-Saltatoria.—In many genera there is well-marked autotomy of the *posterior* or *jumping-legs*, and, as shown by Heineken (*loc. cit.*), Frédéricq (*loc. cit.*), and Contejean (*loc. cit.*), it occurs at the femoro-trochanteric suture. I am indebted to Mr. J. Graham Kerr for the information that, as noticed by him in the Paraguayan Chaco, administration of chloroform to *Tropinotus* readily causes autotomy at the suture. It is uncertain whether a *point d'appui* is necessary in Saltatoria. Till recently it has been supposed that reproduction of the lost legs does not occur in Saltatoria, on which point reference may be made to the writings of Durieu (24), Frédéricq, Peyerimhoff (65), and Werner (79); but Griffini (42, 43, 44) has lately described some captured specimens which seem to indicate that, as in the *Cursoria*, reproduction of the *legs* occurs in some at least of the Saltatoria during post-embryonic development, and that it commences from the femoro-trochanteric suture. In the nymphs of certain forms regeneration of the *antennæ* has been observed by Graber (39), after he had amputated them near the basal joint. He also records that repair occurred in the wing-covers after pieces had been snipped out with scissors.

Orthoptera-Cursoria.—Many Phasmodæ exhibit autotomy of the *legs* during the later periods of immaturity and during the adult state, but our information on the subject is not very extensive. As he has described in an interesting series of papers, Bordage (5, 6, 7, 8, 10) has found that autotomy at the femoro-trochanteric suture was easily obtainable with several different kinds of stimuli, though the latent period between stimulus and rupture was considerably modified by such factors as age, sex, and mode of stimulus. His experiments seem to show that autotomy may occur either with or without a *point d'appui* being employed. Scudder (72) did not observe autotomy in *Diapheromera*, but the mutilated extremity of a leg eventually fell away up to the suture. In these forms reproduction of the limb may occur not only at the suture but from more distal points.

As regards the *legs* of Blattidæ, my previous paper gives the facts which seem to demonstrate that their loss not infrequently takes place by a feebly developed autotomy at the femoro-trochanteric suture. Regeneration may commence at this point or from the stump of either femur or tibia, but not from any part of the tarsus. The stump of this latter region may be retained for some time after mutilation, but it is invariably dry and shrivelled. The *antennæ* of Blattidæ are certainly capable of reproduction. The earliest observations seem to be those of Heineken (46) on *Leucophaea*. He cut off the *antennæ* "near the base," but did not notice the effects of the injury or whether the reproduction

seemed to commence from the two large basal joints or from one of the smaller ones borne by them.

Neuroptera.—Watson (77) has observed that in the larva of *Agrion* amputation of a leg "close to the body" was followed by reproduction by the next ecdysis. Lubbock (54) found that the terminal joints of the *antenna* in nymphs of *Chloëon* were not reproduced.

Lepidoptera.—It is stated that autotomy occurs in the imagoes of certain forms, but as there is no regeneration the point is not of present interest. Several authors have described deformities and reproduction in the *legs* of imagoes after amputation performed on their larvæ or pupæ. But in this group the great uncertainty as to the relationships between the several parts of the larval and pupal appendages and those of the imago presents great difficulties to the study of reproduction. Gonin (37), in a recent revision of the structure of the larval legs just before pupation, concludes that only the extremity of the developing pupal leg projects into that of the larva. Hence amputation of the latter at its base removes only the tarsus of the former, and so on. Till the details of metamorphosis are better understood our knowledge of reproduction of appendages in *Lepidoptera* must remain very slight. Réaumur (71) obtained negative results by amputating the legs in the larva of *Vanessa*; while Newport (61) found that the same method of experiment resulted in either complete or partial development of the injured limbs in the imago. He concluded that regeneration commenced from the seat of injury wherever situated. Mélise (58) agreed with this on the strength of his own experiments on the larva of *Sericaria*. Watson (77) obtained reproduction of the legs in *Platysamia* after injuring those of the larva. In a discussion of the diverse results of Réaumur and Newport, Künckel d'Herculais (49) considers that while the former destroyed the histoblast rudiment of the imago leg, the latter merely mutilated it; but Gonin (37) holds that this explanation is insufficient in view of the non-agreement in position of the similarly named regions of the larval and pupal limbs.

As there can be little doubt that reproduction of the appendages can occur in members of other Arthropod orders than those which have received experimental enquiry, the preceding summary of our present knowledge of how far the power of commencing a new growth is confined to one region or distributed more generally in an appendage is, of course, very incomplete. Enough is known, however, to establish that there is a considerable range of variation in this respect between the members of different orders and to some extent between members of the same order. In cases where autotomy in the strict sense of sudden rupture of a limb either in immediate or almost immediate response to a stimulus is most clearly exhibited, it is a necessary result that reproduction is initiated from one particular point, especially where, as in *Crustacea*, the regenerated region can be seen sprouting from the stump and covered only by a thin cuticle. But in *Tracheata* it is

a more difficult matter to be sure as to the exact starting-point of reproduction and the way in which the new growth is elaborated; for in these forms it does not project beyond the stump, and hence it is visible only at the ecdysis which liberates it. [It is of interest that the comparatively exposed condition of the new growth in Crustacea is correlated with an aquatic habit, and its protected condition with the terrestrial habit of the Tracheata; though only a bare suggestion that contact with hard surfaces, as on land, might more readily injure a new and delicate structure is permissible.] In the occluded condition of the new growth in Tracheates there is necessarily involved a disturbance in the normal relations between the chitinous investment of the stump and the subjacent hypodermis. As development of the regenerated extremity proceeds the hypodermis must slip away from the cuticle and towards the base of the limb, leaving a space occupied by the growing extremity. This structure is formed in a curled up condition, and straightens only on liberation at ecdysis, as was first described by Blackwall (3) in the case of Spiders. [Weismann (78) has shown that in the normal development of *Musca* the leg-rudiments are similarly curled up.] This state of things and the displacement of the internal portions of the stump are illustrated for Blattidæ by figures 1 *a* and 1 *b* (Plate LVIII.). The regenerated tarsus is curled up and occupies half of the chitinous stump of the tibia, while the soft parts of the latter have largely withdrawn into the chitinous femur. I have failed to make a satisfactory dissection of the regenerated leg within the chitinous coxa and trochanter; but in such a case it would seem that the displacement of parts must be more pronounced than in the case illustrated.

It is obvious therefore that in Tracheata regeneration is complicated by the peculiar occlusion of the new growth, and further enquiry is necessary before we can say exactly what is the history of the soft parts of the stump left by amputation, especially as it is still uncertain whether normal ecdysis involves changes more deeply seated than the mere renewal of the cuticle. If that is the case, as seems suggested by such observations as those of Lubbock (54) on the antennæ of *Chloëon* and of Wagner (*loc. cit.*) on Spiders, there is no longer any question as to a "starting-point" of reproduction, for the new extremity would be a part of the general reconstruction and not a bud. On the other hand, the elaboration of the extremity as an outgrowth from the stump is certainly suggested by the already mentioned observations of Newport on *Julus*. It is, however, very possible that the phenomena of ecdysis differ considerably in the several groups.

THE RELATIVE SIZE AND GROWTH OF REPRODUCED APPENDAGES.

The peculiar fact that it is a constant feature of reproduced appendages in certain cases that they differ in structure from the normal congenital appendages they replace will be dealt with later on. At present only the size and growth of the regenerated

structures as a whole will be considered. A regenerated appendage, or part of an appendage, is always smaller than its fellow, provided that the latter is of congenital origin or is a reproduced structure of earlier date. This natural state of things was first understood rightly by Réaumur, the pioneer of the study of reproduction of lost parts. He corrected the assumption of previous authors that such instances were cases of congenital asymmetry. Nearly all accounts of the reproduction of Arthropod limbs agree in stating that if there are still several ecdyses to be accomplished, the reproduced limb grows with special rapidity so as to approximate or equal in size its congenital fellow.

In Crustacea observations in this respect are recorded by certain of the authors already mentioned (17, 18, 68), from which it appears that some of the appendages of Decapods when reproduced attain their normal size more rapidly than do others. There is, however, considerable want of uniformity of result for the same appendage, and Brook has recorded that temperature, the kind of food, &c. are important factors in the matter.

The special rapidity of growth of regenerated appendages in Spiders, Myriapods, Collembola, and Phasmidæ has been recorded in works already referred to, and also by Fortnum (25) in the last-named group.

There is evidence that in Crustaceans the regenerated appendage more frequently attains equality with its congenital fellow than is the case in Tracheates—a feature which perhaps has some explanation in the freer mode of growth seen in the former group.

In Blattidæ my own observations show that the growth of reproduced appendages is very rapid. Measurements were made with a micrometer-eyepiece of a few nymphs of *Stylopyga orientalis* averaging .8 cm. in body-length and therefore quite young, the body-length of an adult being about 2.0 cm., as opposed to a length of .5 cm. in newly hatched young. I measured the total length of the *tarsus* in these .8 cm. nymphs, and the total length of the cast cuticles of the corresponding tarsi just after ecdysis and apparently before any appreciable shrinkage had occurred. In four instances of normal tarsi the average increase of length after ecdysis was 13 per cent., while in four cases of reproduced tarsi the increase was 29 per cent.

An obvious result of the specially rapid growth of a reproduced limb is that the disproportion in size between it and its normal fellow is less in cases where regeneration has occurred early in the life-history than in those in which it has taken place near maturity. For instance, the tarsi of the third pair of legs in 20 adults of *Periplaneta americana*, taken haphazard from individuals in which one of the tarsi was normal and the other reproduced, showed by measurement that if the length of the normal tarsus be taken as 100, the mean length of the reproduced tarsi was 96.5. On the other hand, the mean length of the reproduced tarsi of seven nymphs averaging .53 cm. in body-length was found to be 87.1,

when expressed in a similar manner to the above. [The tarsi in this latter case were not from the third pair of legs only, but this would not appreciably affect the validity of the comparison.] Among adults there are occasional cases in which the difference is much greater than 3.5 per cent., and such probably indicate that loss and reproduction have occurred in the later instars. It was noticed that the disproportion between the reproduced tarsus and its normal fellow was somewhat greater in adults of *Stylopyga orientalis* than in adults of *Periplaneta americana* or *P. australasica*. This may be due to specific differences in the rate of growth of the reproduced structures, or else to some special liability in the first-named species to accidental loss during the later instars. As in Cockroaches the reproduced tarsus has only four joints, it follows that in cases where one tarsus is normal and its fellow reproduced and the two are of approximately equal lengths, the mean lengths of the joints of the latter are on the whole greater than those of the former. In the case of insects with "complete metamorphosis" reproduced appendages in the imago have always been described as smaller than the normal, though it is possible that they may sometimes become symmetrical, for Newport (61) found that in *Vanessa* larvæ reproduction of a leg commenced two stadia before pupation was accompanied by progressive increase in size.

THE STRUCTURE OF THE REPRODUCED LEGS IN THE BLATTIDÆ.

In addition to the general observations on the natural history of ecdysis recorded in my previous paper, the following facts were noticed during the experiments made in the course of the enquiry into the regeneration of the legs in Cockroaches.

(a) *The Length of the Period between Mutilation and Reproduction.*

As already recorded, the legs of 833 nymphs of *Stylopyga orientalis* were mutilated in various parts and the animals kept in confinement in order that the reproduction of the injured limbs might be observed. In 625 cases out of 1473 mutilations, reproduction occurred. The instances tabulated (see p. 934) indicate the *shortest* periods which elapsed between mutilation and reproduction in different degrees. [The term "reproduction" implies in all cases that regrowth of the mutilated or amputated parts took place with the tarsus in a *four-jointed* condition.]

The total number of cases in which it was possible to keep an exact account of the number of days between mutilation and the ecdysis succeeding, and from which the instances recorded in the table were taken, was hardly large enough to permit more than a mere suggestion that reproduction may take place in a shorter time in early nymphs than in nymphs approaching maturity, and that it may take place among the latter more rapidly in males than in females. There is, however, some definite evidence that reproduction of the tarsus alone may occur within a shorter time than that of the more proximal regions of the leg. It is probable that in

TABLE A.

Age or size of individual at the ecdysis which liberated the reproduced appendage.	Number of days between mutilation and ecdysis.	Reproduction took place of the	Lost parts of other legs in the same individual which were <i>not</i> reproduced at this ecdysis.
Body-length 1.9 cm. } (late nymph). }	81	femur downwards.	
Male (final ecdysis).....	84	" "	
Female (" ").....	90	" "	
Body-length .85 cm. } (early nymph). }	43	tibia downwards.	
Male (final ecdysis).....	87	" "	
Female (" ").....	106	" "	
Male (" ").....	70	tarsus.	
Body-length 1.9 cm. } (late nymph). }	81	"	
Female (final ecdysis).....	90	"	
Male (" ").....	82	"	Tibia downwards.
Body-length 2.05 cm. } (late nymph). } ...	102	"	" "
Male (final moult)	83	"	Femur downwards.
Body-length 2.0 cm. } (late nymph). }	87	"	" "

species with a shorter post-embryonic development than *Stylopyga orientalis* reproduction is more rapid. The latter is an unfavourable form for observations of this kind, but was selected as being the species most easily obtainable in large numbers. However long the interval between mutilation and ecdysis, the reproduced legs were always smaller than their normal fellows, nor could I find any particular differences in size between legs reproduced and liberated by ecdysis after short and long periods respectively. The new growths were distinctly dwarf when they appeared after as many as 220 days after mutilation. In a certain number of cases reproduction did not occur even when much longer periods between mutilation and succeeding ecdysis had elapsed than are given in the above table. Thus, amputation at the tibio-femoral articulation or in the middle of the tibia was not followed by any reproduction after intervals of 102, 112, and 192 days. The parts from the femoro-trochanteric suture were not reproduced after an interval of 116 days in another case. In these same instances, however, the lost tarsus of another leg was reproduced, thus favouring the conclusion that there is a relation between the extent of the injury and the time necessary for reproduction. It seems probable that these exceptional cases of non-reproduction after long periods should be attributed to individual causes. The facts that non-reproduction was always total (*i. e.*, that ecdysis left the limb in the same condition as at mutilation) and that when reproduction did occur it was always complete (*i. e.*, the several regions of the

limb right down to its extremity were present and identifiable) are features generally found in Tracheates. It would appear that the formation of the new appendage is a very rapid process, and the facts are favourable to the view that ecdysis really involves more or less reconstruction of the soft parts as well as of the cuticle. This, however, can hardly be the case in Crustaceans, in which the new growth is distinctly a reproduction of the limb while still covered by a cuticle.

(b) *Relative Dimensions of the Tarsal Joints.*

The reproduced femur and tibia resemble those of the normal congenital limb, though they are always smaller than the latter at their first appearance. In one or two cases I have found the tibia of arcuate form, but this condition was probably due to incomplete straightening from the coiled-up condition before ecdysis. The reproduced tarsus is, however, always four-jointed, though in certain very exceptional cases to be shortly described this condition was not quite fully expressed. It is never five-jointed as in the normal.

The general appearance of a normal and of a reproduced tarsus from the same pair of legs of an adult *Periplaneta americana* is shown in Plate LVIII. figs. 2 & 3. The following table gives examples of the relative lengths of the tarsal joints of both normal and reproduced forms. The measurements were made along the dorsal side and with the tarsi as much extended as possible. It is obvious that this method imposes undue prominence on the lengths of the proximal and terminal joints, on account of the telescoping of the intermediate joints into the above and into each other at their articulations, but the results are sufficient for comparison as the treatment was uniform. The tarsi of small nymphs were measured with a micrometer eyepiece, and those of large nymphs with a sliding screw micrometer kindly lent to me by Professor W. F. R. Weldon.

In these tables and later on the several joints of a tarsus or other appendage are for brevity referred to as j_1, j_2 , &c. in the case of normal congenital structures, and as J_1, J_2 , &c. in the case of reproduced structures, the numeration beginning with the proximal joint.

In the following tables the total length of the tarsus was reduced to 100 in each case, and the lengths of the several joints are expressed as percentages.

TABLE B.—*Periplaneta americana*.

5-jointed tarsi. Means of measurements of 115 tarsi from the third pair of legs.

j_1 .	j_2 .	j_3 .	j_4 .	j_5 .
53.2	15.6	9.5	4.9	16.8

4-jointed tarsi. Means of measurements of 115 tarsi from the third pair of legs.

J_1 .	J_2 .	J_3 .	J_4 .
57.4	18.3	6.4	17.9

TABLE C.—*Stylopyga orientalis*.

5-jointed.

4-jointed.

		j_1	j_2	j_3	j_4	j_5		J_1	J_2	J_3	J_4	
Pair I.	Young	38.2	13.9	11.2	7.8	28.3	Mean of 19 cases.	41.5	17.1	10.8	30.2	Mean of 13 cases.
	Adult	40.3	15.5	11.3	7.3	26.3	Mean of 13 cases.	43.9	17.4	9.7	28.6	Mean of 13 cases.
Pair II.	Young	44.7	14.9	10.6	6.7	22.9	Mean of 20 cases.	48.2	17.2	9.0	25.3	Mean of 13 cases.
	Adult	46.2	15.3	10.6	6.3	21.6	Mean of 13 cases.	51.8	17.6	7.7	22.7	Mean of 13 cases.
Pair III.	Young	47.7	16.1	10.6	6.3	18.3	Mean of 20 cases.	51.4	17.5	8.8	21.9	Mean of 15 cases.
	Adult	50.2	16.5	10.5	5.5	17.0	Mean of 13 cases.	55.2	18.1	7.5	18.8	Mean of 14 cases.

The definitely constituted nature of the 4-jointed form of tarsus in both young and adult individuals and on all three pairs of legs is illustrated by Table C, and from the values recorded therein it is obvious that the behaviour of the 4-jointed form is in general agreement with that of the normal tarsus. If the relative values of the several joints in the latter are examined, it is seen that the total length is rather more evenly distributed among the joints in the case of Pair I. than in that of Pair II., and in the case of Pair II. than in that of Pair III. This is most easily seen in the case of the longer joints, j_1 and j_5 , though the shorter intermediate joints are also concerned. In any single individual animal the *total* length of the tarsus is of course greater in Pair III. than in Pair II., and in Pair II. than in Pair I. So that in a longer (more posterior) tarsus j_1 is relatively greater and j_5 relatively smaller than in a shorter (more anterior) tarsus. Now in the case of the 4-jointed tarsi it will be seen that J_1 and J_4 are affected in a similar manner. Again, the values for the 5-jointed tarsi present a strong indication that j_1 is relatively longer in adult than in immature individuals, j_5 being affected inversely. So is it for J_1 and J_4 respectively in the 4-jointed tarsi. The measurements forming the data for constructing Table C were purposely taken from young of all sizes, from newly hatched to over 20 cm. in body-length (penultimate instar); and a consideration of the cases in order of age did not reveal any reliable indication that the above noted alteration in the ratios of j_1 and j_5 was established progressively. The relative increase of j_1 and decrease of j_5 appear to be coincident with the attainment of maturity, and the same is true for J_1 and J_4 . It is admitted that the above statements are based on a comparatively small total of observations, and that

there is difficulty in making very accurate measurements of the shorter intermediate joints; but from a consideration of the individual instances from which the means in Table C were obtained, it is believed that the data are sufficiently reliable to justify what has been said above. It has, moreover, been ascertained that the results are the same when the two sexes are considered separately, as the differences between male and female in the ratios of the several tarsal joints to the whole tarsus are extremely slight, so that the figures tell the same tale whether the two sexes are taken together or separately.

(c) *The Armature of the Tarsal Joints.*

Subject to specific differences the tarsal joints in Blattidæ are provided with a closely-set armature of spines. In addition to the numerous small spines all the joints except the terminal one bear at their distal ends strong spurs or calcares, which are directed ventralwards and outwardly, one on either side. Similar spurs are developed in reproduced tarsi. Examination showed that in both kinds of tarsi the armature is sometimes abnormal. The abnormal conditions met with fall under three heads, as follows:—

- (a) A tarsal joint had more than two spurs. In such cases the commonest condition was the presence of one supernumerary spur on one side.
- (b) A tarsal joint had one of the normal spurs completely absent (there being no scar indicating accidental breaking off).
- (c) A tarsal joint had a spur of normal form placed some distance anteriorly to the proper position at the end of the joint.

The following Table shows the incidence of abnormality observed:—

TABLE D.

		<i>Periplaneta americana.</i>	<i>Periplaneta australasie.</i>	<i>Stylopyga orientalis.</i>
5-jointed tarsi.	Armature normal	15	72	100
	Armature of one or more joints abnormal.....	1	3	0
	Total cases examined.....	16	75	100
4-jointed tarsi.	Armature normal	23	65	46
	Armature of one or more joints abnormal.....	10	6	54
	Total cases examined.....	33	71	100

As in the case of normal spurs, supernumerary ones were always situated on the sides of the tarsal joints and never in the mid ventral line. In all except three cases from *S. orientalis* the supernumerary spurs were placed quite close to the normal spurs. Hence the most common condition—that of *one* supernumerary spur—was expressed as one spur on one side and two on the other. In cases where the total number of spurs on a joint exceeded three there were supernumerary spurs on both sides: for instance five spurs would be expressed as three on one side and two on the other. This tendency to uniformity in the distribution of supernumerary spurs was observed in all cases except in five from *S. orientalis* and one from *P. americana*. In these latter there were either three or four spurs on one side of the joint and only a single (the normal) one on the other. The cases of abnormal armature showed no indication of any relation between the number of supernumerary spurs on a single joint and the extent to which a supernumerary armature occurred in the tarsus as a whole. The joints seemed to vary quite independently of each other in respect of their armature. But on the whole there is obviously a greater frequency of abnormality of the armature in reproduced than in normal tarsi. In this connection it may be noted that Newport observed that the reproduced appendages of Arthropods are particularly liable to disturbances in their armature. Some or all of the normal spines may be absent or there may be supernumerary spines. His observations in this respect were chiefly on Myriapoda and Lepidoptera after injury to the larval appendages. In respect of cases of abnormal armature in the reproduced legs of Blattidæ, it may perhaps be suggested that the additional spines represent the normal terminal armature of a joint whose normal articulation is absent, on the supposition that in the reproduced tarsus one of its four joints is equivalent to two joints of a normal tarsus fused together. There are, however, objections to such a view. The supernumerary spines in 4-jointed as in 5-jointed tarsi were, with only two or three exceptions among all the tarsi examined, grouped closely together in the proper position of the normal spines instead of being situated near the middle of the joint. Moreover, the table (see p. 938) shows the frequent occurrence of tarsi with a supernumerary armature on more than one joint.

(d) *Malformed Tarsi.*

Among the several thousand tarsi examined there were found 10 in which one or more of the articulations were imperfectly formed. The appearance of such cases is sufficiently explained by Plate LVIII. figures 4–10, and they are probably much the same as the “crippled” limbs often found in Coleoptera and other groups. The present cases seem to be reproduced tarsi, though those illustrated by figs. 4 and 10 are perhaps malformed.

“normal” tarsi. The interest of these crippled tarsi lies in their great rarity, their tendency to possess several supernumerary spines, and the fact that the fusions resulting from the incompleteness of the articulations are nearly always confined to the intermediate shorter joints, leaving the proximal and distal joints well-defined.

THE CHARACTERS OF REPRODUCED APPENDAGES IN OTHER
INSECTA AND ARTHROPODA GENERALLY.

Before making a comparison of the normal and reproduced legs of the Blattidæ from a statistical point of view, it is desirable to refer to certain special characters possessed by reproduced appendages in other groups of Arthropods.

The observations of various authors on reproduction of lost appendages in Arthropoda have usually been of but partial nature, and only in a few cases have experiments in this connection been extended over a large number of individuals of the same species.

But the published work is sufficient to indicate that the structures which replace lost or mutilated appendages fall into two main divisions. Moreover, one or the other of these two kinds of reproduction is constantly associated with a particular degree of injury in particular cases of appendages or genera to the entire exclusion of the other kind. In other words, a certain injury to a particular appendage among particular families of genera is invariably followed by reproduction of one kind. The other kind of reproduction is as constantly associated with other cases. The two kinds of reproduction met with are briefly:—

(a) *In all chief respects, such as the number of joints and their relative dimensions, the reproduced appendage is the counterpart of the normal congenital appendage.*

(b) *The reproduced appendage differs from the normal appendage in certain respects which are constant, and in cases where maturity of the animal is attained through a series of ecdyses the special features of the reproduced appendage are perpetuated; so that, strictly speaking, the animal does not reproduce the normal appendage. The chief distinguishing feature of this kind of reproduction is that the number of joints present is less than in the normal appendage.*

THE FOLLOWING CASES FALL UNDER (a):—

CRUSTACEA. *Decapoda*.—Observations on the reproduction of lost appendages appear to have been mainly on the Decapoda. The accounts of authors already referred to agree in stating that the *chela* and *walking-legs* are reproduced by structures resembling the normal in all respects except size. As regards the flagellum of the *antenna*, it is, however, not possible to speak with certainty, for no observer has given any details as to the number of its joints when reproduced. Moreover, the large number of joints of the normal antenna in most cases and the liability to loss of the more distal joints leave the normal numbers for most species somewhat

uncertain. But some degree of circumstantial evidence that the reproduced flagellum has the normal number is afforded by observations (18, 68) that it is very often of equal length with its fellow at the first ecdysis after mutilation.

But that the reproduced appendages of Crustaceans are not invariably replicas of the normal is shown by the experiments of Przibram (67) and by the remarkable cases described by Herbst (48), Hofer (50), and Milne-Edwards (60) of various Decapods replacing an eye by an antenna-like structure. These instances, however, do not fall under (b) above, and for the present must stand apart as isolated cases with special features. Borradaile (11) has recently described certain instances of abnormal *antennae* in *Macrura-Anomala* which may possibly have arisen in connection with reproduction, but these also differ from the cases to be described under (b) in the possession of *more* than the normal number of joints.

Isopoda.—Heineken (47) made a few observations on the reproduction of the *antennae* of a Madeiran *Armadillo*; but his account unfortunately gives no details beyond stating that the new growths were sometimes "perfect" and sometimes "rudimentary."

Cirripedia.—Darwin (22) speaks of the regeneration after injury of the *cirri* (*thoracic limbs*) in *Balanus* as though the new structures were like the normal.

ARACHNIDA. *Araneidae*.—The *pedipalps*, *walking-legs*, and *spinnerets* appear, when reproduced, to be invariably like the normal in all respects except size. Blackwall, however, mentions that if the pedipalp of a male Spider is mutilated between the penultimate and final ecdyses, the sperm-case of the digital (terminal) joint is not developed on the attainment of maturity. This structure, which is distinctive of the adult condition, is produced in cases where mutilation is performed *two* ecdyses before maturity.

MYRIAPODA.—Newport's observations (61) indicate that the *walking-legs*, when regenerated, though of small size, are of normal structure.

INSECTA. *Orthoptera-Saltatoria*.—It appears, from the recent investigations of Griffini (*loc. cit.*), that in this group reproduced legs possess the normal number of joints throughout.

Neuroptera.—Watson (77) found that injury to the *leg* of an *Agrion* larva resulted in the production of a limb of normal aspect at the next ecdysis, except that the claw of the terminal tarsal joint was absent.

UNDER (b) MAY BE PLACED THE FOLLOWING OBSERVATIONS:—

ARACHNIDA. *Scorpionidae*.—The cases of regeneration referred to above as shown to me by Mr. R. I. Pocock were a *Buthus* and a *Scorpio*, both immature. In the former the *leg* had been broken very near the base of the femur, and from this point there grew out a dwarf tarsus with terminal claws of normal appearance. In the latter case a break had occurred in the patella, and borne apparently directly on the seat of injury were a set of small but

normally shaped claws. Mr. Pocock informs me that he has noticed other cases of a similar nature. The production of the normal *terminal* structure, associated with deficiency of proximal parts, as in the above cases, is one of the chief characters of the kind of regeneration defined under (b).

MYRIAPODA.—Newport (61) removed the normal 7-jointed *antenna* of *Julus* by cutting through j_2 close to its base, but without apparently injuring j_1 . At ecdysis a dwarf 6-jointed antenna appeared, each joint being shorter and thicker than the normal, while J_6 closely resembled j_7 . [But section of j_3 resulted at ecdysis in the production of an antenna having 7 joints, an instance of regeneration of the kind described under (a), which is cited in this place for the sake of comparison.]

INSECTA. *Collembola*.—Lubbock (55) amputated the normal 6-jointed *antenna* of *Orchesella* by cutting through j_2 . At ecdysis the antenna was reproduced in a 3-jointed form, which was perpetuated through all subsequent ecdyses observed. J_2 was longer than j_2 , while J_3 was slender and resembled j_6 . In *Tomocerus* the result of pulling out j_4 of the normal 4-jointed antenna was the production and perpetuation of a 3-jointed antenna with J_3 like j_4 . Lubbock's own observations on *Aetheocerus*, and those of de Geer (34), Latreille (53), and Bourlet (14) quoted by him, all tend to show that fewer joints than the normal combined with a resemblance of the actual distal joint to the normal distal joint is the characteristic condition of an antenna when reproduced.

Orthoptera-Saltatoria. Acridiidae.—Griffini (42) describes a *Gomphocerus* in which the *antennae* had almost certainly been reproduced. In this genus the antenna has normally about 23 joints, the 7 terminal joints being clavate. The case described had 9 joints in one antenna and 2 in the other clearly defined, but in each case the terminal joint showed faint constrictions suggestive of incomplete division into from 3 to 5 joints. These terminal joints or series of fused joints were clavate, and so bore a resemblance to the terminal joints of the normal antenna.

Orthoptera-Cursoria. Phasmidae.—In this family the *legs* bear tarsi which are 5-jointed as in Blattidæ, and as in the latter there is ample evidence that when reproduced the tarsus assumes a 4-jointed arrangement. The probability that the latter condition arises in connection with reproduction was first pointed out by Coquerel (20). Previously to this the 4-jointed tarsus in Phasmids had perplexed several entomologists, especially on account of the asymmetry involved by the presence of one or two reproduced legs in otherwise normal individuals. Gray (41) had established the genus *Heteronemia* for specimens of *Bacteria mexicana* with "small hind legs." Westwood (80) had figured a *Cyphocrania* with reproduced tarsi, and devoted a new subgenus (*Craspedonia*) to cases of *Monandropoda inuncans* with 4-jointed tarsi on the anterior pair of legs. The error involved was corrected by Coquerel. Percheron (64) described an *Acanthoderus* and Newport (61) a *Lopaphus* with one or more tarsi 4-jointed.

Scudder (72) seems to have been the first to make experiments on the reproduction of the legs. In *Diapheromera* he found that amputation at any point below the femoro-trochanteric suture resulted in the reproduction of the lost parts with the tarsus in a 4-jointed condition. Bordage's experiments on *Monandropoda inuncans* and *Rhaphiderus scabrosus* show that the reproduced tarsus is invariably 4-jointed in these species. Through the kindness of Dr. David Sharp, I have been able to examine two nymphs of *Anchiale*, recently obtained in New Britain by Dr. A. Willey. Each of these has one leg reproduced with the tarsus 4-jointed. A third specimen is apparently in the same condition, though the tarsal articulations are not clearly defined. In the two former specimens, as in all the cases which have been figured or described in detail by the several authors above named, the terminal joint of the tarsus (J_4) resembles the terminal joint of the normal tarsus (j_5) and possesses the normal double claw. J_1 resembles j_1 , and J_2 and J_3 are like the intermediate joints of the normal tarsus. In view of this evidence it seems not improbable that Fortnum (25) overlooked the tarsus in the case of a *Diura* which he describes as having renewed one of the legs with "all the joints perfect."

Blattidæ.—My own previously published observations that experiment shows that the reproduced legs in this family bear 4-jointed tarsi may be added to the evidence from captured specimens collected by Brisout de Barneville (16), quoted in my previous paper. I have also noticed the 4-jointed tarsus in apparently reproduced legs in *Loboptera*. Newport mentions a *Panesthia* with one tarsus apparently in a 3-jointed condition, which was probably an instance like the "crippled" tarsi in *Stylopyga* described above.

Hemiptera-Heteropoda.—Douglas (23) has described an extensive series of unilateral abnormalities in antennæ which he considers were for the most part the results of reproduction after loss of the normal antennæ. His cases were collected from more than twenty species belonging to the sections Lygaeina, Coreina, and Scutatoria. The characteristic features of the apparently reproduced antennæ were that, whether the normal number of joints was 4 or 5, the abnormal antenna possessed one joint less than the normal, and that the actual terminal joint resembled the normal terminal one. As a rule these antennæ had the intermediate joints of different relative lengths from those of the normal, the most frequent variations being that J_3 was longer than j_2 and J_4 than j_5 . But there was a considerable want of uniformity in the conditions observed. In some cases the antennæ were apparently of normal structure with the terminal joint wanting, while in others with the normal number of joints he found partial fusions between two joints and abnormally short single joints. On the whole it seems probable that while most of the cases were reproductions having the general features described under (b), some of them were merely instances of injured normal antennæ.

Heineken (46) has a single case of the *antenna* of *Reduvius* being regenerated with 3 joints instead of the normal 4 after mutilation in the "pupal" state.

Lepidoptera.—Observations on the regeneration of appendages in this order have yielded results so varied that it is not possible to place them as a whole under either (a) or (b). It has already been pointed out that much more experimental observation, and a clearer understanding of the exact relations borne by the larval and pupal appendages to those of the imago, are necessary before the phenomena of reproduction in this order can be interpreted satisfactorily. The effects of mutilation of the legs of larvæ on those of the imago were first investigated by Réaumur (71), and since his time the subject has attracted only occasional notice. From the small amount of recorded work it is not possible to gather how far the results of a particular kind of injury at a particular stage in the life-history are uniform. The largest number of experiments on a single genus appear to be those of Newport (61) on *Vanessa* larvæ. In the imagos there was much variation in the condition of the injured limbs. In all cases femur, tibia, and tarsus could be distinguished, but the number of tarsal joints varied considerably. In all, however, the terminal claw of the tarsus was present. This fact and the drawings which illustrate his paper suggest that the reproduced tarsus in all these cases should be regarded as representing the whole of the normal tarsus, rather than for instance that a 3-jointed tarsus should be considered as equivalent to three particular joints of the normal tarsus. However this matter be looked upon, it remains that the tarsus is sufficiently represented to bear the normal termination, the claw: so that these observations on *Vanessa* are of particular interest as evidence of the tendency, so characteristic of the instances quoted under (b) above, towards the production of the terminal structure normal to the limb, so that though normality in the number of joints may be wanting, its actual termination is of normal structure. But this tendency is not displayed in *Lepidoptera* with the constancy it possesses in other orders, for the experiments of Mélise (58) on *Sericaria* and of Watson (77) on *Dicranura* gave results contrary to Newport's as regards the tarsal claws. The total number of observations by these two authors was, however, too small for a fair comparison with those of Newport.

But setting aside the *Lepidoptera*, it seems that we have at least some clear indication that in other groups of *Arthropods* in which reproduction has been studied there are two well-defined types of structure assumed by the growths which replace lost appendages, and that in any given case these two kinds are not interchangeable. The reproduced limb either resembles the normal in the number and conformation of its joints, or else it does not do so. Now the interest of the cases in which the reproduced appendage differs from the normal is that the various examples exhibit a considerable degree of uniformity in their abnormal characters—a uniformity which is sufficiently marked to enable us

to say that just as appendages reproduced like the normal are true to a type, so those which differ from the normal are true to a type also, and are not merely irregular and unfinished imitations of the normal structures concerning which it is possible to say "this is the normal structure with such and such a part wanting or malformed." The features leading to the above conclusion are briefly as follows:—

The most prominent is that the number of joints is less than the normal. This numerical difference is, with certain rare exceptions, an actual one and not merely an apparent difference due to such a factor as the presence of incompletely formed articulations. The joints of the appendage are distinctly marked off from each other by articulations of apparently normal completeness. Another character is that in cases where the normal appendage possesses the terminal joint or joints differentiated from the others in length or form, the reproduction has its terminal joint or joints modified so as to in some cases apparently exactly, and in others to approximately resemble those of the normal.

A third character is that the special features are perpetuated through all stadia into maturity, no matter what instar suffered the loss necessitating reproduction. The evidence as to this is, however, not complete in all cases, but there is no record of numerical increase taking place in a reproduced appendage. That this is so is of interest in connection with the fact that in cases where the normal post-embryonic development is prolonged it is characteristic that the number of joints in at least the case of antennæ is progressively increased. At present the evidence suggests that the growth reproducing a lost appendage is without the power of numerical increase. If this is really so, it is necessary to ask whether we are justified in regarding the phenomena of reproduction as equivalent to a simple recurrence of normal development in at all events such cases as those under consideration. In the instance of the reproduced tail of Lizards we know that it is not. If the regeneration of a Tracheate limb is a process of budding, there is at least one difference between a congenital and a reproduced limb—viz., that the former arises as an outgrowth from the trunk, while the latter is a product of the basal part of the limb itself and so is not a regrowth of the entire limb. If, on the other hand, ecdysis involves reconstruction of the soft parts, the regeneration of a lost appendage must be brought about by changes more like those which usher in each successive stadium under normal circumstances.

It has been suggested from time to time that such departures from the normal as have been described above should be regarded as equivalent to normal appendages with one or more joints omitted, and sometimes it has been sought to identify particular joints of the normal as absent in the reproduced limb; but these suggestions have rested on the general appearance of the latter and not on statistical comparisons of the features of the normal and reproduced structures.

So far as the tarsus of the Blattidæ is concerned, reference to tables B and C, giving the ratios for the several joints of the 5-jointed and 4-jointed forms, seems to forbid such an explanation of the condition of the latter. This is evidently divided up in a manner peculiar to itself. A like conclusion follows a comparison of the actual length of the joints of two tarsi of the same total length and from the same pair of legs of one individual, when one is 4-jointed and the other 5-jointed. And with regard to other cases, a consideration of the descriptions and figures of the authors whose work I have quoted does not support the view that we can explain numerical deficiency on the ground that any *particular* joint of the normal appendage is absent in such and such an instance. The structure of the reproduced appendage being what it is, seems to render this kind of explanation meaningless, as Bateson (2) has already pointed out in commenting on the reproduced tarsus of *Periplaneta*. There is perhaps more to be said for the view put forward by some, that these abnormal reproduced structures contain the representatives of one or more joints of the normal limb fused together and that hence arises the numerical deficiency. But such an explanation demands that a certain joint of the reproduced limb should be equivalent in length to the sum of two or more joints of a normal limb of the same total length. But in the case of the tarsi of Blattidæ the measurements already quoted show that here at least such an explanation is inadmissible. It is true that the number of individual cases included in the tables was not large, but it may be held to have been large enough to demonstrate that it would be exceedingly exceptional for the sum of any two joints of the normal tarsus to even approximate the length of a single joint of the reproduced tarsus, for the measurements given contain no example of this kind. We may suppose that J_1 and J_4 correspond with j_1 and j_5 respectively on account of their structural characters and position, but there is nothing to establish that J_2 and J_3 represent either $(j_2 + j_3) + j_4$ or $j_2 + (j_3 + j_4)$ —a result which shakes confidence in the identification of the longer proximal and terminal joints with those of the normal. This matter also has been already discussed by Bateson in the place cited, and it is enough to add that his conclusion that the four joints of the reproduced tarsus collectively represent the five joints of the normal, which was based on measurements of *Periplaneta* only, is borne out by those of *Stylopyga* made more recently.

The view that such reproduced structures should be looked upon as intrinsically on a different plan from the normal structures they replace, rather than as abortive attempts at the exact reproduction of those normal structures, finds support not only on the grounds already set forth, but in some cases at least from the closeness of the variation of their individual parts. In the case of *Periplaneta americana* measurements of the lengths of the tarsal joints were made in 115 normal and 115 reproduced tarsi. These tarsi were all from the third pair of legs of adult individuals. The total length of each tarsus was reduced to 1.000 and the lengths of the

individual joints expressed correspondingly as fractions. The values so obtained were then arranged in ascending order in their own series, and those occupying the positions of the first, second, and third quarterly divisions noted. Following the terminology of Galton (31) these are indicated by Q_1 , M , and Q_3 respectively. The probable error of variation of the series from its mean value will then be expressed by Galton's formula $\frac{Q_3 - Q_1}{2}$.

TABLE F.—*Periplaneta americana*.
Five-jointed tarsus.

	J_1 .	J_2 .	J_3 .	J_4 .	J_5 .
Q_1	·521	·152	·095	·046	·162
M	·529	·156	·099	·049	·168
Q_3	·535	·160	·101	·051	·174
Mean error as percentage of M }	1·3	2·6	3·0	5·0	3·6

Four-jointed tarsus.

	J_1 .	J_2 .	J_3 .	J_4 .
Q_1	·565	·178	·060	·172
M	·575	·183	·064	·177
Q_3	·584	·189	·068	·183
Mean error as percentage of M }	1·6	3·0	6·2	3·1

It will be seen that the percentage variation of the several joints is very little greater in the case of the reproduced than in that of the normal tarsi. Too much reliance should not be placed on the results obtained for the smaller joints, as in their case the errors of observation are necessarily greater proportionately. At the same time it is probable that we are justified in accepting the indication that these joints are in a somewhat less stable condition than the proximal and terminal joints, for the above result goes hand in hand with the facts elicited from a consideration of the cases of "malformed" tarsi already described.

Subsequently to the construction of the above table, which has already been published (2), with the kind assistance of Mr. Alfred Harker I tested the closeness of the correlation between certain of the joints by the method devised by Galton (32). This method deals with the relations between any two parts of a structure whose dimensions are capable of expression by numbers, and its

application to the present case reads as follows:—For every unit of absolute length that a particular tarsal joint deviates from the mean length of such joints in the series examined, any other joint selected will on the average deviate from the mean length of such joints to the extent of x units and in the same direction. [x would be equivalent to unity only in the hypothetical case of the two joints always varying exactly together, or, in other words, exhibiting an absolute correlation.]

TABLE G.—*Periplaneta americana*.

5-jointed tarsi.

The deviation of j_1 from its mean being 1.0, the mean of the corresponding				deviations of j_2 from its mean was .52.
"	j_1	"	"	1.0, the mean of the corresponding
"	j_2	"	"	deviations of j_3 from its mean was .72.
"		"	"	1.0, the mean of the corresponding
"		"	"	deviations of j_5 from its mean was .31.

or, expressed conversely,

The deviation of j_2 from its mean being 1.0, the mean of the corresponding				deviations of j_1 from its mean was .52.
"	j_3	"	"	1.0, the mean of the corresponding
"	j_5	"	"	deviations of j_1 from its mean was .72.
"	j_3	"	"	1.0, the mean of the corresponding
"		"	"	deviations of j_2 from its mean was .31.

4-jointed tarsi.

The deviation of J_1 from its mean being 1.0, the mean of the corresponding				deviations of J_2 from its mean was .70.
"	J_1	"	"	1.0, the mean of the corresponding
"	J_2	"	"	deviations of J_3 from its mean was .66.
"		"	"	1.0, the mean of the corresponding
"		"	"	deviations of J_4 from its mean was .49.

or, expressed conversely,

The deviation of J_2 from its mean being 1.0, the mean of the corresponding				deviations of J_1 from its mean was .70.
"	J_4	"	"	1.0, the mean of the corresponding
"	J_4	"	"	deviations of J_1 from its mean was .66.
"		"	"	1.0, the mean of the corresponding
"		"	"	deviations of J_2 from its mean was .49.

The number of cases on which the above results are based is of course much smaller than is usually adopted for the consideration of normal correlated structures on such lines, but it serves to show the similarity of behaviour of the two kinds of tarsi. The specially rapid growth of regenerated appendages has been referred to already, and the following observation on *Periplaneta* emphasizes the specialized nature of the regenerated limb by indicating that the rate of growth is controlled according to the age of the animal at the time of injury.

20 adults of *P. americana* were found with the third pair of legs bearing on one side a normal and on the other a 4-jointed tarsus. The percentage difference in total length of the tarsi of the two kinds averaged only 3.5, an amount not appreciable to the naked eye. Now it is not at all likely that in all these cases the repro-

duced tarsi had started in the same instar, so it is evident that their growth, always more rapid than that of the normal structures, must have been subject to a special trophic control whereby those which commenced their existence in the later instars grew more rapidly than those of earlier origin. In a series of *Stylopyga orientalis* there is, however, less evidence of such a special control, for there is usually a well-marked difference in size between a reproduced tarsus and its normal fellow in adult specimens as well as in young.

But this species affords an additional illustration of the specialized nature of the reproduced tarsus; for, as has already been shown in Table C, the several joints undergo changes in their relative proportions at the attainment of the animal's maturity in the same directions as do those of the normal.

It seems probable that a statistical examination of the reproduced legs of Phasmidæ would yield much the same results as above; but there is as yet not sufficient evidence to justify a statement that the reproduced antennæ of Myriapoda, Collembola, and Hemiptera have so high a degree of specialization. It is possible that there are intrinsic differences in the two kinds of appendages in their response to particular injuries. It has already been pointed out that injury to the basal joints of an antenna in some forms may result in numerical deficiency with its correlated peculiarities, while the removal of distal portions alone is followed by their regrowth with normal features.

In this connection it is of interest that the more basal antennal joints seem to be specially concerned in the formation of new articulations in certain forms which progressively increase the number of joints through the sequence of the ecdyses [Termitidæ (40), Ephemeridæ (54), Phasmidæ (73)]. And in the rare case of a diminution in the number of joints with advancing age described by Lubbock (54) as occurring in nymphs of *Chloëon*, it is the 4th joint of a 20-jointed antenna which amalgamates with itself the three joints distal to it.

But admitting that there is greater variability in reproduced antennæ, it is clear that when they differ from the normal they do so in the same kind of way as do the legs of Phasmidæ and Blattidæ, and with them form a series of instances standing in remarkable contrast with those in which the reproduced appendages are replicas of the normal. The causes which promote these differences of behaviour in allied groups are for the present quite obscure.

So also are we in the dark as to the factors which give constancy to a growth which arises sporadically and has not been represented in the normal ontogenetic development. It is surely therefore somewhat meaningless to apply to such cases terms like "throwing back" and "reversion," as has been done by certain authors. It is indeed true that reproduced parts in various animals display characters similar to the normal characters of corresponding parts in presumably allied genera. Perhaps the best known of such

instances is that afforded by the scaling of the reproduced tail in certain Lizards (12, 13). In a recent note Giard (36) has collected instances of this kind of variation under the title of "hypotypic regeneration," and has included thereunder the 4-jointed reproduced tarsus of Blattidæ and Phasmidæ. In the suggestion that such structures are really reversions to ancestral forms he is followed by Bordage (6).

Such a view must be based on the assumption that the normally 4-jointed tarsus of Lepismidæ and Locustidæ represents the primitive condition in Insecta, the grounds for which being that the Lepismidæ are usually held to be primitive forms and that the reproduced tarsus in Locustidæ does not exhibit any reduction in the number of its joints. But the tarsus of Insects as known to us is characteristically *five*-jointed, and our ignorance of the meaning of the phenomena known as reversions denies much weight to arguments supported by appeal to them.

Our present knowledge of the whole subject of reproduction after injury is so scanty as to render of very minor value such arguments as that "it is advantageous for a mutilated individual to abridge the process of reproduction and not to recapitulate in their entirety all the phylogenetically ancestral stages." Have we indeed any justification at all for supposing that reproduction of any part is a recapitulation of even the normal ontogeny? In the cases already described only one seems to afford any degree of suggestion that reproduction involves a throwing back of normal development, and that is the observation of Blackwall that male Spiders do not develop the adult sperm-case of the terminal joint of the pedipalp when that appendage has been mutilated between the penultimate and final ecdyses. But this peculiarly adult structure is not a distinct joint, and the instance is one in which a certain identifiable part of the normal appendage is absent, and so is unlike the instances in which the reproduced growth is a completely functional structure but differs from the normal in the arrangement of its parts generally.

It is of much interest in connection with the peculiarities of reproduction forming the subject of this paper, that departures from the normal in the main similar to them have been observed in genera the nature of whose developmental history, and the fact that the abnormal condition was frequently manifest symmetrically on the two sides, seem to render it most unlikely that reproduction had occurred. Cases of this kind in antennæ of certain Hymenoptera and Coleoptera have been commented on by Bateson (2. p. 411); and though in some of the examples the variation in the number of antennal joints was so great that the normal number remained uncertain, the following features occurred not infrequently. Where the terminal joint or joints were in the normal of specialized structure, the exceptional cases of few-jointed antennæ presented a similar condition. Moreover there were usually departures from the normal in the relative lengths of the other joints, and the joints were usually of longer individual lengths than those

of the normal. Garbowski (33) has more recently described a case in *Hygrocarabus* where a leg was similarly affected, and Bateson's series of examples from the antennæ of *Forficula* (2. p. 413) seem for the most part to belong to the same category. In this genus the number of antennal joints is usually 14, though specimens with only 13 or 12 joints are not infrequent. Bateson found that in 13- and 12-jointed examples j_3 was markedly and j_4 somewhat longer than the corresponding joints in 14-jointed examples. In the case of 18 antennæ from adults measured by myself, 12 had 14 joints, 3 had 13, and 3 had 12. In the 13- and 12-jointed specimens j_3 was of about the same length as in the 14-jointed specimens, but in 5 out of the 6 j_4 was distinctly longer than in 14-jointed specimens. Among the 6 cases of few-jointed antennæ the more distal joints were longer than the joints in the same positions in 14-jointed specimens in 3 instances, and of practically the same lengths in the other 3 instances. So that here again is manifest the tendency for the appendage with abnormally few joints to approximate the total length of the normal by increasing the lengths of its individual joints. As *Forficula* is an orthopterous insect it is of course quite possible that some of these cases of few-jointed antennæ arose in connection with reproduction. Bateson inclined to the belief that the symmetrical condition of many such cases indicated a congenital origin at least occasionally. But in the light of the evidence that in Blattidæ the mechanism of reproduction is able to bring about symmetry in size between a normal and a reproduced tarsus on the same pair of legs and between two reproduced tarsi on the same pair, it seems possible that a similar compensating control may exist over other cases of reproduction. In their general features these exceptional antennæ of *Forficula* approach the certainly reproduced antennæ of Myriapoda and Collembola on the one hand, and the abnormal and apparently congenital antennæ of certain Hymenoptera and Coleoptera on the other. But much more evidence regarding the reproduction of the antennæ in a series of selected forms must be forthcoming before we can say anything as to the relationships between these peculiar appearances when seen in genera with such different life-histories.

In cases where the departures from the normal structural arrangement are known to have arisen as reproductions, it is of course permissible to regard them as in some sense analogous with bud-variations in plants; and as in their case, so also in that of arthropod appendages, the idea has been advanced that the disturbances seen are the results of insufficient and unequal nutrition. Though no doubt the removal of an appendage does produce an unusual demand on the nutritive channels directed to it, it would appear that any failure to deal with the special circumstances of the case is expressed rather in the small size of the reproduced structure than in its morphological features. For it is characteristic of the Tracheate groups at least that if any new growth at all is revealed at the ecdysis succeeding injury, it is in a sense a complete appendage and not an amorphous bud. The mechanism

of reproduction executes the proper work however much or however little may be the amount of material placed at its disposal. The suggested factor of insufficient nutritive supply is moreover no explanation of why in some genera or groups of genera the new growth is constantly a true "reproduction" in that it exactly resembles the normal, while in other genera or groups of genera it as constantly assumes a form which is strikingly different from the normal. And granted that parts subject to loss have their reproduction ensured by a special adaptation of the nutritive and trophic supplies appropriated to them, there is no solution yet possible of why reproductions which are unlike the normal should exhibit a degree of fixity and trueness to type which in the case of normal congenital structures we are accustomed to regard as the outcome of selection.

In summary of what has been said it seems to be the case that:—

(i.) In Arthropoda generally the power of reproducing a lost or injured appendage is partial in so far that the basal portion of the appendage must be left to inaugurate the new growth, reproduction of the entire appendage by the trunk being not possible.

(ii.) The power of reproduction seems to be possessed concurrently with the ecdyses and to be relinquished when these no longer occur.

(iii.) In Crustacea the reproduced portion of an appendage can be observed growing out from the stump, being covered with a thin cuticle specially formed over it. In Tracheata the reproduced portion does not become revealed till ecdysis, being entirely hidden by the cuticle of the region proximal to the place of amputation. There is some evidence that in many cases the elaboration of the reproduced portion is a rapid process taking place only just before ecdysis.

(iv.) Subject to certain objections to regarding the reproduced appendage of a Tracheate Arthropod as invariably of the nature of a bud from the stump, in some forms reproduction may commence from almost any part of any joint, while in others autotomy or else the dropping away of portions of the stump subsequently to injury determines that reproduction shall commence only from very few regions or even only from a single region.

(v.) In Crustacea the reproduced portion of an appendage is, with reservations as to certain doubtful and exceptional cases, an exact counterpart of the congenital structures it replaces. This is also constantly the case with certain appendages in certain Tracheata.

(vi.) In certain appendages of some Tracheata the reproduced portion is constantly unlike the normal, being distinguished therefrom mainly as follows:—

- (a) The number of joints is less than those which have been lost, and is one less in cases where the normal number is not more than six.

- (b) The joints of the reproduced portion have relative dimensions which are different from those of the normal joints and render any scheme of identity therewith of doubtful value.
- (c) If the terminal joint or joints of the normal appendage are differentiated from those more proximal, then the terminal joint or joints of the reproduction are similarly differentiated in spite of their want of agreement in numerical sequence with the joints of the normal.

(vii.) The peculiar distinguishing features of reproductions unlike the normal are perpetuated through all subsequent ecdyses, the normal structure not being reassumed at any time.

(viii.) The reproduced portion of an appendage, whether it is of the type exactly resembling the normal or of the type which differs therefrom as above described, possesses the power of growing with special rapidity, so that, always smaller than its congenital fellow on its first appearance, it sooner or later attains a symmetrical size, provided that this is not prevented by the cessation of general growth.

(ix.) The structural characters of reproductions which are unlike the normal often possess a high degree of organic stability, and in some cases at least a degree which is quite comparable with that possessed by the characters of the congenital structure the reproduction takes the place of. To account for this high stability in a reproduced structure by the operation of selection seems impossible.

(x.) In the instance of such a reproduction afforded by the 4-jointed tarsus of Blattidæ, so established is the nature of the reproduced appendage, that when the animal possessing it attains maturity, the relative proportions of its joints undergo the same kind of change as that which is normal in the congenital form of tarsus. It is thus obvious that a reproduction of this kind may not only possess a structural stability comparable with that of the normal, but also be dominated by a trophic control so specialized that the changes proper to the several stadia are brought about in the reproduced just as they are in the congenital appendage, being unimpeded by the profound structural differences between the two.

I must express my thanks to Mr. Adam Sedgwick for placing at my disposal the facilities of the Zoological Laboratory at Cambridge for this work, and to Mr. W. Bateson, not only for the suggestion which incepted the inquiry, but for kind advice and criticism during its progress.

References to Literature.

1. BATE, C. SPENCE.—“Report of the Committee appointed to explore the Marine Fauna and Flora of the South Coast of Devon and Cornwall.” No. 2. Brit. Assoc. Rep. 1868, p. 283.
2. BATESON, W.—‘Materials for the Study of Variation,’ 1894, pp. 63 & 415.

3. BLACKWALL, J.—“Report on some recent Researches into the Structure, Functions, and Economy of the Araneidea made in Great Britain.” Brit. Assoc. Rep. 1845, p. 62.
4. BODIER.—“Sur la Reproduction des Pattes des Crabes.” Observations sur la physique, etc., de Rozier, 1778, xi. p. 33.
5. BORDAGE, E.—“Phénomènes d'Autotomie observés chez les Nymphes de *Monandropoda inuncans* et de *Rhaphiderus scabrosus*.” Comptes-rendus Acad. Sci. 1897, cxxiv. pp. 210 & 378.
6. BORDAGE, E.—“Sur la Régénération tétramérique du Tarse des Phasmides.” Comptes-rendus Acad. Sci. 1897, cxxiv. p. 1536.
7. BORDAGE, E.—Régénérations chez les Phasmides après des sections artificielles et non autotomique.” Bull. Soc. Entom. de France : séance du 13 juillet, 1898.
8. BORDAGE, E.—“Sur les localisations de Régénérations chez les Phasmides.” Comptes-rendus Soc. de Biologie : séance du 30 juillet, 1898.
9. BORDAGE, E.—“Sur le mode probable de formation de la Soudure fémoro-trochantérique chez les Arthropodes.” Comptes-rendus Soc. de Biologie : séance du 30 juillet, 1898.
10. BORDAGE, E.—“De l'influence de certaines conditions sur la régularité de la Régénération tétramérique chez les Phasmides.” Comptes-rendus Soc. de Biologie, octobre 1898.
11. BORRADAILE, L. A.—“On some Crustaceans from the South Pacific : Part II. *Macrura Anomala*.” Proc. Zool. Soc. 1898, p. 457.
12. BOULENGER, G. A.—“On the Scaling of the Reproduced Tail in Lizards.” Proc. Zool. Soc. 1888, p. 351.
13. BOULENGER, G. A.—“On an Iguana with Reproduced Tail.” Proc. Zool. Soc. 1891, p. 466.
14. BOURLET, L'ABBÉ.—“Mémoires sur les Podures.” Mém. de la Soc. Roy. des Sci. Lille, 1839 ; and Trans. de la Soc. d'Agricult. du Départm. du Nord : Douai, 1841-42.
15. BRINDLEY, H. H.—“On the Regeneration of the Legs in the Blattidæ.” Proc. Zool. Soc. 1897, p. 903.
16. BRISOUT DE BARNEVILLE.—Ann. de la Soc. Entom. 1848, sér. 2, vi. Bulletin, p. xix.
17. BROOK, G.—“Notes on the Reproduction of Lost Parts in the Lobster (*Homarus vulgaris*).” Proc. Roy. Phys. Soc. of Edinburgh, 1887, p. 370.
18. CHANTRAN, M.—“Nouvelles Observations sur le Développement des Écrevisses.” Comptes-rendus Acad. Sci. 1871, lxxiii. p. 220.
19. CONTEJEAN, C.—“Sur l'Autotomie chez la Sauterelle et le Léopard.” Comptes-rendus Acad. Sci. 1890, cxi. p. 611.
20. COQUEREL, C.—“Orthoptères de Bourbon et de Madagascar.” Ann. Soc. Entom. de France, 1861, sér. 4, i. p. 495.
21. COUCH, J.—“On the process of Exuviation and Growth in Crabs and Lobsters.” Trans. Cornwall Polytech. Soc., 1843.
22. DARWIN, C.—‘Monograph of the Cirripedia,’ 1854, p. 158.

23. DOUGLAS, J. W.—“On some peculiarities in the Development of Hemiptera-Heteropoda.” *Ent. Month. Mag.* 1865, ii. p. 270; 1866, iii. p. 200; 1876, xiii. p. 188; 1895, xxxi. p. 144.
24. DURIEU, A.—“Notes sur quelques Orthoptères.” *Petites Nouv. Entomol.* 1876, no. 158.
25. FORTNUM.—*Trans. Entom. Soc. London*, 1845–47, iv. p. 98.
26. FRÉDÉRICQ, L.—“Amputation des Pattes par mouvement réflexe chez le Crabe.” *Archiv. de Biologie*, 1882, iii. p. 235.
27. FRÉDÉRICQ, L.—“Sur l'Autotomie ou Mutilation par voie réflexe comme moyen de défense chez les Animaux.” *Archiv. de Zoologie Expér.* 1883, sér. 2, i. p. 413.
28. FRÉDÉRICQ, L.—“L'Autotomie chez les Étoiles de Mer.” *Rev. Scientif.* 1887, sér. 3, xiv. p. 589.
29. FRÉDÉRICQ, L.—“Les Mutilations spontanées ou l'Autotomie.” *Rev. Scientif.* 1886, sér. 3, xii. p. 613.
30. FRÉDÉRICQ, L.—“La lutte pour l'existence chez les Animaux marins,” 1889. [“Autotomie chez les Insectes,” p. 258.]
31. GALTON, F.—“Natural Inheritance,” 1889, Chap. v.
32. GALTON, F.—“On Co-relations and their Measurements.” *Proc. Roy. Soc.* 1888–89, xlv. p. 137.
33. GARBOWSKI, T. H.—“Aberrations in the Structure of Appendages in the Coleoptera.” *The Entomologist*, April 1895, p. 125.
34. DE GEER, C.—*Act. Soc. Reg. Sci. Upsala*, 1740, p. 64.
35. GIARD, A.—“L'Autotomie dans la Série animale.” *Rev. Scientif.* 1887, sér. 3, xxxix. p. 629.
36. GIARD, A.—“Sur les Régénérations hypotypiques.” *Comptes-rendus Soc. de Biologie*, 1897, sér. 10, iv. p. 315.
37. GONIN, J.—“Recherches sur la Métamorphose des Lépidoptères.” *Bulletin de la Soc. Vaudoise des Sci. Naturelles*, 1894, sér. 3, xxx. p. 122.
38. GOODSIR, H. D. S.—“A short Account of the mode of Reproduction of Lost Parts in the Crustacea.” *Ann. & Mag. Nat. Hist.* 1844, ser. 1, xiii. p. 67, and *Brit. Assoc. Rep.* 1844.
39. GRABER, V.—“Zur Entwicklungsgeschichte und Reproductionsfähigkeit der Orthopteren.” *Sitzungsb. der k. Akad. der Wiss. Wien, Math.-naturw. Cl. lv. Bd. i.* 1867; and *Ann. & Mag. Nat. Hist.* ser. 3, xix. p. 147.
40. GRASSI, B., & SANDIAS, A.—“Costituzione e Sviluppo della Società dei Termitidi.” *Catania*, 1893, p. 25; and *Quart. Journ. Microsc. Science*, 1896, xxxix: part 3, p. 245.
41. GRAY, G. R.—“Synopsis of the Phasmidæ in the British Museum,” p. 19.
42. GRIFFINI, A.—“Di un *Pristes tuberosus* anomalo.” *Boll. dei Musei di Zool. ed Anat. comp. Torino*, 1896, xi. no. 234.
43. GRIFFINI, A.—“Di due *Acrididi* anomali.” *Boll. dei Musei di Zool. ed Anat. comp. Torino*, 1896, xi. no. 256.
44. GRIFFINI, A.—“Descrizione d'una nuova *Pseudofillide* del Però e osservazioni sopra una anomalia del tipo di questa

- specie." Boll. dei Musei di Zool. ed. Anat. Comp. Torino, 1898, xiii. no. 328.
45. HALLEZ, P.—"Un mot d'historique à propos de l'Amputation réflexe des Pattes chez les Crustacés." Bulletin Sci. du Nord, 1886, sér. 2, xvii. p. 342.
 46. HEINEKEN, C.—"On the Reproduction of Members in Spiders and Insects." Zool. Journ. 1829, iv. p. 284.
 47. HEINEKEN, C.—"Experiments and Observations on the Casting-off and Reproduction of the Legs in Crabs and Spiders." Zool. Journ. 1829, iv. p. 422.
 48. HERBST, C.—"Über die Regeneration von antennenähnlichen Organen an Stelle von Augen." Archiv f. Entwicklungsmechanik, 1895, ii. p. 544.
 49. D'HERCULAIS, KÜNCKEL.—'Recherches sur l'Organisation et le Développement des Volucelles,' 1875, p. 160.
 50. HOFER, B.—"Ein Krebs mit einer Extremität statt eines Stielauges." Verhandl. d. deutschen zool. Gesellschaft, 1894, p. 82.
 51. HOWES, G. B.—"On the Reproduction of the 'Feeler' of the Lobster's Antenna." Journ. Anat. & Physiol. 1882, xvi. p. 47.
 52. HUXLEY, T. H.—'The Crayfish,' 1881, p. 38.
 53. LATREILLE.—"Organisation extérieure et comparée des Insectes de l'Ordre des Thysanoures." Nouv. Ann. du Muséum d'Hist. Nat. 1832, i. p. 186.
 54. LUBBOCK, J.—"On the Development of *Chloëon* (*Ephemera*) *dimidiatum*." Trans. Linn. Soc. 1864, p. 61, and 1866, p. 477.
 55. LUBBOCK, J.—'Monograph of the Collembola and Thysanura,' 1873, p. 60.
 56. MACCULLOCH.—"On the means by which Crabs throw off their Claws." Quart. Journ. of Science, Literature, and Arts of the Royal Instit. 1826, xx. p. 1.
 57. MCCOOK, H. C.—Proc. Acad. Nat. Sci. of Philadelphia, 1883, p. 196; and Journ. Roy. Microsc. Soc. ser. 2, iv. p. 225.
 58. MÉLISE.—Ann. de la Soc. Entomol. de Belgique, 1879, xxii., Comptes-rendus, p. xxi; and Proc. Entomol. Soc. London, 1879, p. xxxii.
 59. MILNE-EDWARDS, H.—'Leçons sur la Physiologie et l'Anatomie comparée de l'Homme et des Animaux,' 1863, viii. p. 299 *et seq.*
 60. MILNE-EDWARDS, H.—"Sur un cas de Transformation du Pédoncule oculaire en une Antenne, observé chez une *Laugonste*." Comptes-rendus Acad. Sci. 1864, lix. p. 710.
 61. NEWPORT, G.—"On the Reproduction of Lost Parts in Myriapoda and Insecta." Phil. Trans. 1844.
 62. NEWPORT, G.—"On the Reproduction of Lost Parts in the Articulata." Mag. of Nat. Hist. 1847, ser. 1, xix. p. 145.
 63. PARIZE, P.—"L'Amputation réflexe des Pattes des Crustacés." Rev. Scientif. 1886, sér. 3, xi. p. 379.





Fig. 3.



Fig. 2.

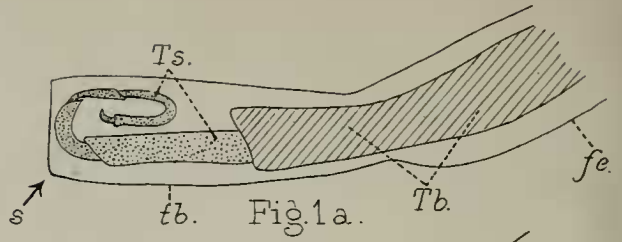


Fig. 1a.

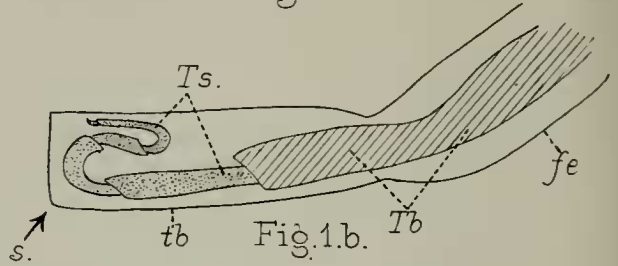


Fig. 1b.



Fig. 4.

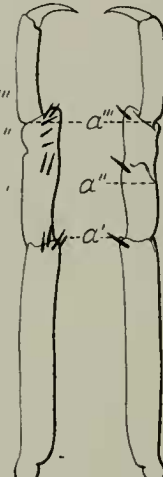
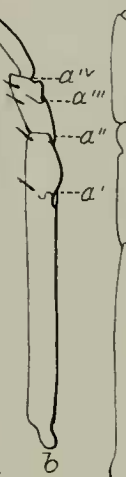


Fig. 5.



Fig. 6.



Fig. 6.



Fig. 7.



Fig. 8.



Fig. 9.



Fig. 10.

